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Differential Contribution of Indigenous Men and Women to the Formation of an Urban Population in the Amazon Region as Revealed by mtDNA and Y-DNA

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ABSTRACT The human populations of the Brazilian Amazon were formed by interethnic crosses between Europeans, Africans, and Amerindians. The relative contribution of men and women of different ethnic groups was not homogeneous, since the social policies of the first three centuries of Brazilian colonization encouraged mating between European men and indigenous women and, later on, African women. In order to test this model based on historical data, we compared the relative contribution of the Y-DNA and mtDNA of Amerindian and non-Amerindian populations to the formation of the urban population of the town of Belém, in the Amazon region, on the basis of a C→T mutation at locus DYS199 present in 90% of the Amerindian Y-DNA and of five markers that define 99% of the mitochondrial sequences of Amerindians. The contribution of indigenous men to the formation of this population was less than 5%, whereas the contribution of indigenous women was estimated at more than 50% of the mitochondrial sequences of the same population. Thus, the present results demonstrate that the contribution of indigenous women to the formation of the Belém population was 10 times higher than the contribution of indigenous men, a genetic consequence of social behavior and attitudes of the past; our results also help clarify the process of integration of indigenous communities into the urban societies in Brazil and possibly in other countries. Am J Phys Anthropol 109:175–180, 1999.

The human populations of the Brazilian Amazon region provide excellent material for genetic investigation because they were formed by interethnic crosses between three groups, i.e., the European colonists mainly represented by the Portuguese, descendants of Africans, and the native Amerindians. The population admixture was not homogeneous in terms of number of individuals that composed the parental stock of each group or in terms of the relative contribution of men and women of different ethnic groups, especially with respect to Europeans and indigenous individuals.

The estimates of the indigenous population size before the beginning of colonization are quite controversial, ranging from 1–8.5 million for South America, from 1–6.8 million for Brazil, and from 1–5 million for the Amazon region (Carneiro-da-Cunha, 1992). After less than four centuries, the occupation of the Amazon region resulted in the

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disappearance of a large part of the indigenous societies and in the reduction of their population to less than 300,000 individuals living today. The European-Indian admixture started soon after the arrival of the first colonists. The social attitude during the first three centuries of Brazilian colonization always encouraged mating between European men and indigenous women and, later, African women. The assimilation of indigenous females was stimulated as a strategy for the occupation of the region, and soldiers who would marry a native were rewarded with land, weapons, and money (Cruz, 1973).

The first Portuguese colonists settled in the Brazilian Amazon region at the beginning of the 17th century, with the founding of the town of Belém in 1616. Since their major objective was the protection of the territory against foreign invasions, the first colonizers were soldiers and volunteer adventurers seeking wealth, rather than families of farmers. The number of Europeans who migrated to the region up to the beginning of the 19th century corresponded to one tenth the number of imported African slaves and one hundredth the estimated number of indigenous people living in the region (Cruz, 1973).

African slaves arrived in the Amazon region in considerable numbers only much later, starting from the second half of the 18th century. The number of slaves imported by 1820 was estimated at approximately 53,000. In contrast to the Portuguese, the Africans sent to the region arrived in family groups and were thus incorporated into urban societies (Salles, 1971).

If a type of preferential mating of European males with non-European females continued for a relatively long period of time, coinciding with the formation and expansion of urban communities, these populations would be expected today to continue to present profound dissimilarities in terms of DNA inherited exclusively from the father (Y-DNA) or from the mother (mt-DNA). In order to test this model based on historical data, we compared the relative contribution of the Y-DNA and mtDNA of Amerindian and non-Amerindian populations to the formation of a population in the Amazon region. To determine patrilineal ancestry, a C→T mutation at locus DYS199, which is present in 90% of the Amerindian Y-DNA (1 marker), was investigated. To determine matrilineal ancestry, five markers that define 99% of the mitochondrial sequences of Amerindians (2–6 markers) were examined.

TABLE 1. Restriction sites and the 9-bp deletion that define the seven mitochondrial lineages analyzed in the present study[1]

Marker	Lineage						
	I	II	III	IV	V	VI	VII
9 bp del	+	+	−	−	−	−	−
*Hpa*I 3,592	+	−	NT	NT	NT	NT	NT
*Hae*III 663	−	−	+	−	−	−	−
Alu 5,176	+	+	+	−	+	+	+
*Hinc*II 13,259	+	+	+	+	−	+	+
*Alu*I 10,397	−	−	−	+	+	+	−

[1] NT, not tested.

MATERIALS AND METHODS

Specimens

We investigated 155 individuals from the town of Belém, located in the northeastern part of the Brazilian Amazon region, with a population of about one million. The samples were collected randomly from blood donors and from individuals who came for parentage tests, and they were not genealogically related.

Methods

Blood specimens were collected in acid citrate dextrose solution, and DNA was extracted from the buffy coat layer of cells using the salt-out procedure (Miller et al., 1988). Polymerase chain reaction (PCR) was carried out using conditions and primers previously described (Underhill et al., 1996; Stone and Stoneking, 1993; Torroni et al., 1993a). The amplified product (3–6 markers; see Table 1) was digested with specific enzymes according to the manufacturer's instructions (Promega), and the digestion product was visualized under ultraviolet (UV) light after electrophoresis on 1.5% agarose gel (6 markers) or 7% polyacrylamide gel (3–5 markers). The 9-bp deletion in region V of the mtDNA was detected by the size of the amplified DNA segment, i.e., 112 bp or 121 bp. The presence of the C or T allele in segment DYS199 was determined by allele-specific PCR (Underhill et al., 1996) followed by electrophoresis on 2% agarose gel.

RESULTS

mtDNA variation

The five polymorphic mtDNA sites studied were selected because, separately or together, they identify more than 99% of the mitochondrial sequences of Amerindian origin. Additionally, we investigated the presence of the *Hpa*I site at position 3,592 in the 22 individuals carrying the 9-bp deletion in order to differentiate the Amerindian mitochondrial sequences from the sequences of African origin. Joint observation of the six polymorphic sites permitted the identification of seven lineages, five of which originated from Amerindians (lineages II–VI, Table 1).

The results are summarized in Table 2. Lineage I is of African origin and was identified in 4 individuals in the sample. This lineage is characterized by the presence of the 9-bp deletion, together with the presence of a *Hpa*I site at position 3,592, which defines the most frequent haplogroup among African populations (Chen et al., 1995). Lineage II (haplogroup B of Amerindians), identified in 18 individuals (11.6% of the sample), has the 9-bp deletion and does not have the *Hpa*I restriction site. Lineage III is characterized by the presence of the *Hae*III restriction site at position 663 and corresponds to haplogroup A of native Americans. This lineage was identified in 34 individuals (21.9%), which compares with 16.7% in contemporary Amazonian Amerindians, but varies from 5% among Surui to 90% among Waiampi (Santos et al., 1996). Lineages IV–VI share the mutation that gives origin to the *Alu*I site at position 10,397. The $AluI_{5176}$ site is also absent in lineage IV, which corresponds to haplogroup D of Amerindians. This lineage was shared by 10 individuals and had a frequency of 6.5% in the Belém population. Lineage V is defined by the presence of the position 10,397 *Alu*I site and by the absence of the position 13,259 *Hinc*II site, and corresponds to Haplogroup C of Amerindians. This lineage was shared by 29 individuals (17.4%). Lineage VI was shared by 2 individuals (1.3%). This lineage has the *Alu*I site at position 10,397, but it does not present any of the mutations that define the most prevalent Amerindian haplogroups (A–D); it may represent additional Asian founding lineages in Native American populations which occur at low frequencies, or haplotypes that belonged to haplogroups C or D and lost their diagnostic markers. Lineage VII is formed by the set of mitochondrial sequences that did not present any of the mutations specifically belonging to Amerindian populations. Since lineages I and VII are present exlusively in non-Amerindian populations and haplotypes II–VI occur only in Amerindians, the population admixture was estimated directly on the basis of the proportions of Amerindian and non-Amerindian lineages.

TABLE 2. Mitochondrial and Y-DNA markers in the population of Belém as compared with Black, White, and Amerindian populations

	Non-Amerindians			Belém	
	Europeans (%)	Africans (%)	Indians (%)	Number	%
mtDNA					
Lineage I	0.0	8.2	0.0	4	2.6
Lineage II	0.0	0.0	20.5	18	11.6
Lineage III	0.0	0.0	16.7	34	21.9
Lineage IV	0.0	0.0	20.8	10	6.5
Lineage V	0.0	0.0	37.0	27	17.4
Lineage VI	0.0	0.0	5.0	2	1.3
Lineage VII	100.0	91.8	0.0	60	38.7
Total	100.0	100.0	100.0	155	100.0
DYS199					
T	0.0	0.0	90.0	4	3.8
C	100.0	100.0	10.0	101	96.2

Y-chromosome variation

In parallel, we investigated the Y-DNA-specific polymorphism of locus DYS199 in the 105 males that composed the sample. The result showed that allele DYS199T, which is specific for native American populations, was present in only 4 individuals (3.8% of all men) in the sample, whereas allele DYS199C was present in the Y-DNA of 101 individuals from Belém (96.8% of the sample).

DISCUSSION

On the basis of mtDNA and Y-DNA markers, we demonstrated a differential contribution of men and women of Amerindian origin to the formation of an urban population of the Amazon region. For this purpose, five Amerindian mtDNA markers and one Y-DNA marker were used.

The 9-bp deletion in the region V of mtDNA is frequent (10.5%) among Amerindians from the Amazon region (Torroni et al., 1993a; Bailliet et al., 1994; Bianchi et al., 1995; Santos et al., 1996; Ward et al., 1996; Easton et al., 1996) and in the rest of the American continent (Torroni et al., 1992, 1993a,b, 1994; Santos et al., 1994; Lorenz and Smith, 1994; Monsalve et al., 1994; Torroni and Wallace, 1995), Asian populations (Stoneking et al., 1990; Ballinger et al., 1992; Harihara et al., 1992; Passarino et al., 1993; Merriwether and Ferrel, 1996), and in Polynesian populations (Hagelberg and Clegg, 1993; Hagelberg et al., 1994; Lum et al., 1994; Redd et al., 1995). The deletion is present at a mean frequency of 8.2% on the African continent (Vigilant et al., 1991; Chen et al., 1995; Soodyall et al., 1996), and is practically always accompanied by the presence of the *Hpa*I restriction site at nucleotide position (np) 3,592, which characterizes the most frequent haplogroup among Africans (haplogroup L) (Chen et al., 1995). The distribution of the 9-bp deletion on different continents suggests that this deletion may have occurred independently many times in Asia, Australia, Oceania, and Central Africa (Melton et al., 1995; Redd et al., 1995; Sykes et al., 1995; Betty et al., 1996; Soodyall et al., 1996), and that region V of mtDNA may be a hot spot for mutations (Barrientos et al., 1995). This indicates that the 9-bp deletion alone should not be used as an anthropological marker (Chen et al., 1995).

Of the ethnic groups that participated in the formation of the Belém population, only Africans and Amerindians may have effectively contributed to the observed frequency of the 9-bp deletion. The genetic backgrounds associated with the 9-bp deletion in Africans and Amerindians are quite distinct. In the present study, we considered the samples with the 9-bp deletion in which the *Hpa*I site at position 3,592 was not present to have originated from the indigenous populations of the region. The result was that, of the 22 mtDNA carrying the 9-bp deletion, 18 (11.6%) were of Amerindian origin and 4 (2.6%) were of typically Africans origin. Lineage I occurs primarily in Pygmy and Southern and Eastern Bantu populations (Soodyal et al., 1996), and is absent in African-Americans of North America. Its presence in the population from Belém is not surprising, because the Brazilian Black population has an origin which is different from that of the equivalent USA and Caribbean populations (Zago et al., 1992).

The frequency of lineage III, defined by the presence of *Hae*III$_{663}$, was the highest among all lineages considered to be of Amerindian origin in the Belém population (21.9%). This mutation is considered to be specific of Asian populations or of their descendants, since it was not described outside Asia or the New World (Torroni et al., 1993b; Merriwether et al., 1995). This mutation defines haplogroup A, which has a mean frequency of 33.2% among Amerindians of North America, Central America, and South America, a higher value than the mean (16.7%) observed among the Amerindian populations of the Amazon region (Torroni et al., 1993a; Bianchi et al., 1995; Santos et al., 1996; Ward et al., 1996). The absence of the mutation that creates the *Hae*III$_{663}$ site in European and African populations and the fact that the contribution of Asian populations (such as the Japanese, for example) to the formation of Amazon populations is considered to be quite limited, indicates that all the mtDNA included in lineage III in the present sample originated from the Amerindians of the region.

The absence of the *Hin*II restriction site in np 13,259 and of the *Alu*I site in np 5,176 defines the Amerindian C and D haplogroups, respectively. Both mutations have been detected in non-Asian populations, but not when accompanied by the presence of the *Alu*I site in np 10,397 (Merriwether et al., 1995). Mutation *Alu*I$_{10,397}$ is frequent in populations of East Asia, Australia, and Melanesia, and among native Americans (Passarino et al., 1996a,b), and it was detected in only one African individual (Chen et al., 1995), probably representing an isolated mutational event. Among Amerindians, +*Alu*I10,397 accompanies all mtDNA sequences belonging to haplogroups C and D (Torroni et al., 1993a,b; Santos et al., 1996), and has been used to define as Asian, Amerindian sequences that do not belong to any of the A–D haplogroups (Bianchi et al., 1995; Merriwether and Ferrel, 1996; Forster et al.,

1996). In the analysis of the Belém population, we used the approach of investigating jointly the presence of the *Alu*$I_{10,397}$ site and of the genetic markers that define haplogroups C (-*Hinc*$II_{13.259}$) and D (-*Alu*$I_{5,176}$), so as to guarantee that these sequences are of Amerindian origin. The result was that 39 of the 155 individuals investigated (25.2%) had the *Alu*I_{10397} restriction site. Of these, 27 (lineage V, 17.4%) belonged to haplogroup C; 10 (lineage IV, 6.5%) belonged to haplogroup D; and 2 (lineage VI, 1.3%) had none of the mutations that characterize haplogroups C and D. In investigations of the mtDNA of Amerindians, the presence of a haplotype that cannot be assigned to any of the prevalent haplogroups (A–D) is not uncommon, but is frequently associated with gene flow among populations (Torroni et al., 1993a,b). Amerindian non A–D haplotypes, when associated with typically Asian mutations as is the case for *Alu*$I_{10,397}$, are denoted "other" haplotypes (Torroni et al., 1993a). Haplotypes such as those observed here may possibly represent mitochondrial lineages present among pre-Columbian natives with reduced prevalence, which were incorporated into the urban populations and which today cannot be identified among the indigenous groups living in the region, or they may simply represent a more common haplotype with an addtional mutation which caused the loss of a diagnostic marker.

The C→T transition on the DYS199 locus of chromosome Y is an excellent indicator of the indigenous contribution. The DYS199T allele is absent in populations from Europe, Africa, Asia, and Oceania, has a frequency of more than 90% among South American and Central American natives, and has a slightly lower frequency (about 50%) among North American natives (Underhill et al., 1996). Similar results were obtained by Rodriguez-Delfin et al. (1997) in studies of the Y-DNA of five Amerindian tribes from the Amazon and of Brazilian Blacks, Whites, and Japanese: the DYS199T allele was present in 87% of the Y-DNA of Amerindians and absent in all other population groups studied.

The comparison of Y-DNA and mtDNA data obtained for the Amazonian population was used to estimate the percentage of the contribution made by indigenous men and women, respectively, to a present-day urban population. On the basis of the frequency of allele DYS199T in Amazonian tribes, we estimated that the contribution of indigenous men to the formation of the Belém population was quite reduced, i.e., less than 5%. The percentage of the contribution of indigenous women was estimated at 59.4% on the basis of the proportion of all typically Amerindian sequences (lineages II–VI) in relation to the total number of sequences investigated. In contrast, the mean Amerindian contribution to the gene pool of more than 5,000 individuals of 10 Amazonian towns based on 13 autosomically coded protein systems was estimated at 41% by Santos and Guerreiro (1995). Further studies, employing additional markers, are necessary to clarify the specific contribution of European and African men and women to the non-Amerindian gene pool of this population.

Thus, the present results demonstrate that the contribution of indigenous females to the formation of the Belém population was 10 times higher than the contribution of indigenous men. These results demonstrate the genetic consequences of a social policy of the past and help clarify the process of integration of indigenous communities into the urban societies that were formed in Brazil (these results may also be applicable in many other countries).

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